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RELATIONSHIPS BETWEEN SPECIES TRAITS AND ECOSYSTEM PROCESSES IN BRACKISH AQUATIC PLANT COMMUNITIES

Charlotte Angove

DOCTORAL DISSERTATION

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The archipelago of the northern Baltic Sea contains shallow, submerged soft sediments that are colonised by diverse aquatic plant communities. Such diverse communities are valuable assets for investigating the relationships between species traits and ecosystem processes, to understand the ecology of submerged aquatic plants. This thesis constitutes three experiments conducted *in situ* using SCUBA in the northern Baltic Sea. The purpose of these experiments was to investigate how plant biomass production is related to plant functional traits, growth strategies, and functional diversity, as well as the role of infauna to plant functional trait-productivity relationships. Overall, results showed that plant functional diversity can be related to productivity likely by selecting for light capture traits, that the finite sediment nutrient source was likely affected by plant biomass-driven demands, and finally infauna can affect plant functional trait-productivity relationships. Overall, by using plant trait and functional diversity investigations, this thesis has improved the collective understanding of submerged aquatic plant functioning.

ABSTRACT

Aquatic plant meadows provide a variety of global ecosystem services. Their populations are declining globally. To conserve and restore aquatic plant meadows and the services which they provide, it is necessary to understand their ecology. A key approach which allows us to explore plant ecology is to investigate the relationships between plant functional traits and ecosystem processes. By investigating plant functional traits, it is possible to develop insights about functional diversity and plant growth strategies. In this thesis, plant functional traits, functional diversity and plant growth strategies are used to investigate aquatic plant biomass production responses to the environment. A series of manipulative experiments were conducted *in situ* in submerged aquatic plant meadows of the northern Baltic Sea using SCUBA. Firstly, the role of plant traits, species identity and sediment porewater NH_4^+ availability for plant nitrogen uptake rates were investigated using a short-term (3.5 h) nitrogen enrichment experiment (Chapter I). Secondly, a 15-week transplant experiment was conducted to explore plant functional trait and functional diversity relationships to productivity (Chapter II). Finally, a similar experiment with additions of the bivalve *Limecola balthica* (12 weeks) was conducted to investigate infauna effects to plant functional trait–productivity relationships (Chapter III). Chapter I showed that short-term nitrogen uptake rates from the sediment were driven by plant-biomass related demands. Similarly, results suggested that plants likely drained ammonium availability from their adjacent sediment porewater. Overall, Chapter I parameterised the possible unfulfilled potential for larger temperate aquatic plants to cycle nutrients. Chapter II results showed strong relationships between productivity and traits which enhanced light capture (height and leaf area). Leaf tissue $\delta^{13}C$ and functional richness were also related to community productivity. The relationship between height and productivity was likely exacerbated by a competitive height interaction between the tallest and second tallest species. Overall, functional richness was related to community biomass production, likely by selecting for traits

which enhanced light capture (selection effect) with potential consequences to carbon supply. Findings support inferences from previous studies of aquatic plant communities which showed that height is strongly related to aquatic plant productivity and trait identity may be more descriptive for primary production compared to functional diversity indices. Chapter III results showed Specific Root Length (SRL) exhibited the strongest relationship to productivity. Leaf area was also related to community production and Median Maximum Root Length (MMRL) exhibited a marginally non-significant relationship to productivity. SRL exhibited collinearity to species identity, therefore it was not possible to interpret SRL effects separately to other traits which may coincide with species identity. Community SRL was related to community shoot frequency, not aboveground biomass production. SRL and shoot proliferation both represent strategies to enhance nutrient absorption from the sediment. Relationships between plant leaf tissue nutrient concentrations (N (% DW), $\delta^{15}N$, $\delta^{13}C$) and *L. balthica* condition index suggested that *L. balthica* affected the sediment nutrient supply and enriched the plants with nutrients. Overall, Chapter III showed that infauna, common in aquatic plant meadows, can change aquatic plant trait-productivity relationships and thus arguably the drivers for submerged aquatic plant community growth. Findings of this thesis can be applied to a variety of other temperate submerged aquatic plant communities. Targeted research questions could contribute to further understanding of submerged aquatic plant ecosystem ecology, including the ecology of monocultures. This thesis summary suggests updating the current description of context-dependent seagrass biomass responses to sediment nutrient enrichment. It proposes a model which, once tested, would help to improve predictive modelling for submerged aquatic plant biomass responses to future change. Also, results of this thesis contribute towards increasing effectiveness of future management by providing insights to infauna effects on plant functioning. This is beneficial to current restoration development because infauna additions to submerged aquatic plant meadows are an option for increasing seagrass restoration success and seagrass resilience to

future change. This thesis identifies that there is requirement for further research in seagrass meadows which form dense root-rhizome mattes, and it describes potential options for future research. It also recommends isotope-tracing experiments and compound-specific isotope tracing experiments to better understand mechanisms of nutrient exchange between infauna and temperate submerged aquatic plants. It has empirically shown current limitations of global plant trait syntheses and it identifies constructive steps forward to improve the global perspective of plant trait ecology. Finally, this thesis advocates the value of insights gained from data-rich functional diversity experiments and plant functional trait experiments. To conclude, this thesis has improved the collective understanding of temperate aquatic plant ecosystem functioning.

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ORIGINAL PUBLICATIONS AND AUTHOR'S CONTRIBUTION

1. Angove C., Norkko A., Gustafsson C., 2018. Assessing the efficiencies and challenges for nutrient uptake by aquatic plants. Journal of Experimental Marine Biology and Ecology, 507 pp. 23–30.
2. Angove C., Norkko A., and Gustafsson C., 2020. The fight to capture light: Functional diversity is related to aquatic plant community productivity likely by enhancing light capture. Frontiers In Marine Science, 7(140) pp. 1-13.
3. Angove C., Norkko A., Gustafsson C. Infauna change the drivers for aquatic plant growth in the northern Baltic Sea. Manuscript.

Table 1. Division of labour for co-authored work that constitutes the thesis by the doctoral candidate C. Angove. CA: Charlotte Angove, CG: Camilla Gustafsson, AN: Alf Norkko.

Thesis chapter	Planning	Field work	Laboratory analysis	Data analysis	Writing
1	CA, AN, CG	CA, CG	CA	CA, AN, CG	CA, AN, CG
2	CA, AN, CG	CA, AN, CG	CA	CA, AN, CG	CA, AN, CG
3	CA, CG, AN	CA, AN, CG	CA	CA, CG, AN	CA, CG, AN
Summary					CA

CONTENTS

DEFINITIONS

Eutrophication	: An increase in the rate of supply of organic matter to an ecosystem (Nixon 1995)
Plant functional trait	: A measurable, heritable, morpho-physio-phenological plant characteristic which can be related to plant fitness (Garnier et al. 2016)
Functional diversity	: The variety of processes which contribute to a function (Garnier et al. 2016)
Functional richness	: The sum of variability of all measured traits in a community (Schleuter et al. 2010)
Functional divergence	: Position of species trait clusters amongst the variability of traits (high values caused by trait clustering and/or traits distributed towards edges of trait variability) (Schleuter et al. 2010)
Functional evenness	: Regularity of trait distribution within a community (Schleuter et al. 2010)
Plant growth strategy	: A regime of resource investments across traits which achieves fitness in response to one or more selective pressures (Guo et al. 2018)

1. INTRODUCTION

Submerged aquatic plant meadows, including seagrass meadows, provide a variety of global ecosystem services (Green & Short 2003, Nordlund et al. 2016). For example, seagrass are such effective carbon sinks (Kennedy et al. 2010, Duarte et al. 2010) that they constitute an important global carbon stock (Fourqurean et al. 2012). Aquatic plant meadows provide many other ecosystem services, such as water purification, recreational fulfilment, and habitat provision for wildlife such as commercially important fish species (García-Llorente et al. 2011, Nordlund et al. 2016). However, aquatic plants are affected by anthropogenic pressures including reduction of water quality (O'Hare et al. 2018), localised pressures such as anchor scars (Ceccherelli et al. 2007, Collins et al. 2010) and global warming (Marba & Duarte 2010, Arias-Ortiz et al. 2018).

Submerged aquatic plants are being lost from lakes at accelerating rates (Zhang et al. 2017). In marine environments, seagrass meadows have been declining at a global scale for more than a century, with evidence of their decline since early quantitative recordings in 1879 (Waycott et al. 2008). Indeed, the total coverage of seagrass is expected to have declined by 29% between 1879 and 2006 (Waycott et al. 2008). Seagrass and other aquatic plants will likely face further challenging conditions in the future (IPCC 2019). During aquatic plant decline, there are consequences of losing the services which they would otherwise provide (e.g. Fourqurean et al. 2012), therefore it imperative to protect and restore aquatic plant ecosystems such as seagrass meadows (Orth et al. 2006). To protect and restore aquatic plant ecosystems, it is essential to understand how aquatic plant biomass production is affected by the environment (Unsworth et al. 2014). Plant functional traits are well-established tools for understanding how plants interact with their environment (Perez-Harguindeguy et al. 2013, Levine 2016), however there are large knowledge gaps about their role to submerged aquatic plant ecosystem functioning.

1.1. Plant functional traits

A plant functional trait is a measurable morpho-physio-phenological characteristic of a plant which can enhance a process that is linked to its fitness, for example biomass production (Violle et al. 2007, Kattge et al. 2011). It is also essentially heritable (Garnier et al. 2016). A plant trait can enhance biomass production by improving access to resources, for example plant height increases the ability for plants to capture and compete for light (Díaz et al. 2004), and root architectural properties can enhance access and utilisation of the sediment nutrient pool (Aerts 1999).

1.2. Plant growth strategies

A plant growth strategy is a regime of resource investments across traits which achieves fitness in response to one or more selective pressures (Guo et al. 2018). Plant growth strategies can describe plant life history strategies (Kautsky 1988, Sabbatini & Murphy 1996, Guo 2018) or, at a smaller scale, strategies that enhance a process related to plant fitness, for example strategies which enhance biomass production (Ezz 2009, Paul et al. 2004). This thesis focuses on the latter use of the term. Studies which investigate plant growth strategies are largely based on the interpretation of traits, for example multiple trait-productivity relationships (e.g. Ezz 2009, Paul et al. 2004, Guo et al. 2018) or qualitative trait comparisons (Kautsky 1988, Sabbatini & Murphy 1996). Therefore, it is possible to use aquatic plant traits to interpret aquatic plant growth strategies, for example investigating the strategies which benefit biomass production by examining many trait-productivity relationships.

1.3. Functional diversity

Functional diversity is an application of plant functional traits to understand advanced attributes to ecological functioning (Hooper et al. 2005). Functional diversity is a concept that evaluates the variety of processes which contribute to functioning (Garnier et al. 2016). There are many scales of functional diversity, for example functional diversity of genes within an individual, individuals

within a species, or species within a community (Garnier et al. 2016). The functional diversity of a submerged aquatic plant community could potentially be increased by a greater diversity of species, for example a greater diversity of root traits. With an increased variability of root traits, communities would likely include both smaller, finer roots as well as longer roots, which exploit nutrients differently from the sediment nutrient pool (Campbell et al. 1991). Functional diversity can increase community productivity (Hooper et al. 2005) by enhancing the complementarity of resource use (complementarity effect), or by increasing the likelihood that individuals with favourable traits are present (selection effect) (Loreau & Hector 2001). Increased species diversity can enhance functional diversity by introducing a greater variability of traits which species manifest.

1.4. Plant functional traits at a global scale

Functional trait research has advanced so much that traits and growth strategies can be compared globally across ecosystems, and these studies can include a mixture of terrestrial and aquatic plants (e.g. Diaz et al. 2015, Pierce et al. 2017, Kattenborn et al. 2017). However, we cannot holistically interpret aquatic plant ecology from these analyses because the relationships between traits and functions are different for aquatic plants compared to terrestrial plants. For instance, the leaf trait specific leaf area (SLA, leaf area per unit leaf biomass), is not necessarily correlated to aquatic plant growth rate, contrary to its function for terrestrial plants (Cambridge & Lambers 1998). Despite this, leaf traits in aquatic plants can be comparable to terrestrial plants on a quantitative scale (Pierce et al. 2012), but there are limitations to their quantitative comparison because their ecological functions are likely to be different. For example, there is limited evidence that SLA enhances light absorption, unlike for terrestrial plants (Ralph et al. 2007). Rather, in submerged aquatic plants SLA exhibits species-specific responses to changes in light (Ralph et al. 2007) and carbon availability (Ow et al. 2015). This shows how plant traits might participate different roles for functioning of aquatic plants

compared to terrestrial plants, and more research is needed to understand aquatic plant trait-productivity relationships.

Aquatic plant traits have been misrepresented in global plant trait syntheses, for example height has been reportedly not applicable to aquatic plants (Pierce et al. 2012, 2017), whereas it is strongly related to temperate aquatic plant productivity (Bornette et al. 1994, Doledec & Statzner 1994, Gustafsson & Norkko 2019). Meanwhile, leaf area has been interpreted as important for leaf energy dynamics and water balance (Diaz et al. 2016), but there are not the same implications for water balance to submerged aquatic plants. Therefore, global trait syntheses have included submerged aquatic plant data, but their inferences are not global because trends have been inferred from a terrestrial plant perspective. Therefore, to properly generalise results to the global plant population, it is necessary to incorporate submerged aquatic plant ecology to global plant syntheses. This highlights the importance for recognising and understanding the ecology of submerged aquatic plants because their interaction with the environment is under-represented, despite their ecological importance. By achieving a greater understanding of submerged aquatic plant ecology, it would be possible to empirically test the global understanding of plant trait ecology which have been developed based on terrestrial ecosystems.

1.5. Resources for submerged aquatic plants

Temperate submerged aquatic plants inhabit marine, estuarine and limnic environments (e.g. Hoang et al. 2016, Arnold et al. 2017, Zhang et al. 2017). One of the most influential factors which affect whether aquatic plants can colonise an area is wave exposure (Hemminga & Duarte 2000). Likewise, wave exposure affects aquatic plant biomass production (Worm 2000, Gustafsson & Norkko 2019). Another major factor which affects aquatic plant biomass production is light availability (Longstaff & Dennison 1999, Ruiz & Romero 2001, Boström et al. 2004, Gustafsson & Boström 2013, Salo et al. 2015). It can affect plant depth distribution (Ralph et al. 2007) and its limitation can reduce plant

growth, shoot density, survival, as well as biomass investments for light capture (Longstaff & Dennison 1999, Ruiz & Romero 2001, Boström et al. 2004, Gustafsson & Boström 2013, Salo et al. 2015). The relationships between aquatic plant functional traits and productivity change with variation of different environmental factors (Arthaud et al. 2012, Gustafsson & Norkko 2019) e.g. selective pressure for aquatic plant height increases with depth (Fu et al. 2014). The relative effects of different environmental factors to productivity are not yet fully understood. Nutrient availability is influential to aquatic plant biomass production (Pérez et al. 1991, Ferdie & Fourqurean 2004, Armitage et al. 2011).

1.6. Aquatic plant nutrient availability

Submerged aquatic plants absorb nutrients from the water column and the sediment, and their reliance on either source can vary depending on relative nutrient concentrations (Touchette & Burkholder 2000). Nutrient enrichment in the sediment and water column can become toxic to plants if nutrient concentrations become too high (Govers et al. 2014, Moreno-Marín et al. 2016). Otherwise, if concentrations do not reach toxic levels plant growth increases if nutrients were previously limiting (Figure 1, Cabaço et al. 2013). Nutrient supply in the water column has a consequence to light availability because it can catalyse micro- and macro- algal blooms which shade plants, which is part of the process of eutrophication (Figure 1, Dennison et al. 1989, McGlathery 2001, Gustafsson et al. 2012).

Eutrophication has varying definitions between studies, e.g. a natural aging process for lakes (Rast & Thornton 1996), or cultural eutrophication is an overloading of nutrients to aquatic systems by anthropogenic activity (Burkholder et al. 2007). This thesis includes a generalised process-based definition suggested for coastal ecosystems, by Nixon (1995): 'An increase in the rate of supply of organic matter to an ecosystem'. Eutrophication has deleterious impacts to aquatic plant communities (e.g. seagrass, Cardoso et al. 2004). One of its main consequences to seagrass is light attenuation by macroalgae, epiphytes and planktonic blooms

(Burkholder et al. 2007). Direct physiological plant responses to water column eutrophication may also contribute to seagrass decline, such as ammonium toxicity and internal carbon limitation which leads to inhibition of nitrate uptake from the water column (Burkholder et al. 2007).

Nutrients in the sediment porewater do not have the same immediate consequences for light availability like the water column source. Therefore, the sediment porewater and water column nutrient source have different ecological consequences to aquatic plants, and it is important to evaluate plant interactions with either source separately. By doing this, it is possible to understand how plants interact with their nutrient sources and the ecological implications of such interactions. Therefore, it is important to explore plant trait-process relationships relating to the sediment nutrient source.

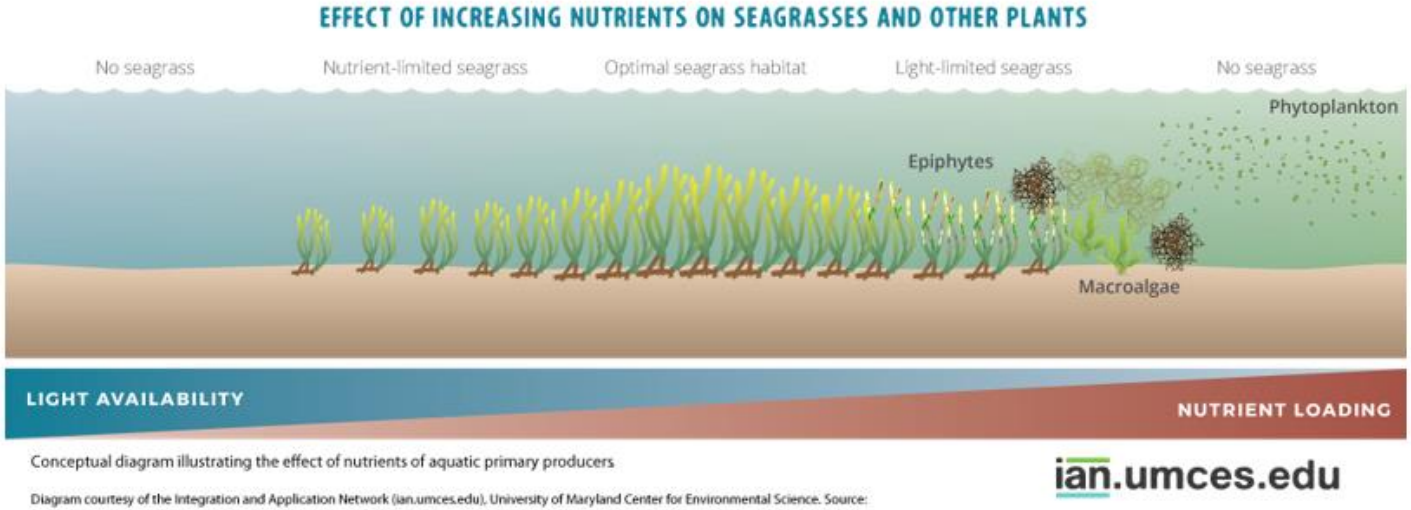

Figure 1. Conceptual diagram illustrating the effect of nutrients in the water column to aquatic primary producers. Diagram courtesy of the Integration and Application Network (ian.umces.edu), University of Maryland Center for Environmental Science, Source "Maryland Coastal Bays 2016: Land and bay perspectives", Jane Thomas.

1.7. Plant functional traits and the sediment nutrient pool

Carbon and nitrogen availability can limit temperate seagrass productivity (Vitousek & Howarth 1991, van Lent et al. 1995, Buapet et al. 2013). Phosphorus availability is more likely to limit productivity of communities which inhabit highly carbonated sand (Short et al. 1985, Broderson et al. 2017). Sediment porewater nutrient enrichment can increase aquatic plant biomass production if nutrient availability was previously limiting productivity (Duarte 1990). However, such responses depend on a variety of environmental factors. Udy & Dennison (1997) and Touchette & Burkholder (2001) developed four categories which described context-dependent seagrass responses to sediment nutrient enrichment (Table 1).

Table 1. Four categories of seagrass response to sediment nutrient enrichment. Categories I-III suggested by Udy & Dennison (1997) and category IV suggested by Touchette & Burkholder (2001).

Response category	Growth response	Physiological response	Environmental context
I	Positive	Positive	Low-nutrient environment where nutrients limited plant growth
II	No response	Positive	Low-nutrient environment where other factors limited plant growth
III	No response	No response	High nutrient environment where nutrient supplies were in excess
IV	Negative	Negative	High nutrient environment where nutrient supplies were in high excess and nutrient additions had detrimental effects to plant growth

Sediment porewater enrichment can change relative plant biomass investments for light capture (Lee & Dunton 2000). For example, sediment nutrient enrichment can affect the relative plant biomass investment in aboveground and belowground biomass (Lee & Dunton 2000, Maurer & Zedler 2002, Fraser et al. 2016).

For example, leaf biomass and aboveground: belowground biomass ratios can increase in response to nitrogen fertilisation of the sediment if nitrogen was previously limiting (Lee & Dunton 2000). Such changes in biomass investment suggest that the sediment nutrient source could affect trait-productivity relationships and plant growth strategies.

Both aquatic and terrestrial plants can facilitate a variety of strategies to access nutrients from the sediment nutrient pool. For instance, they might invest their biomass production into belowground biomass in nutrient poor zones (e.g. Lee & Dunton 2000). They can actively forage for nutrients by shoot and root proliferation (Campbell et al. 1991, de Kroon & Mommer 2006, Kembel et al. 2008, Furman et al. 2017) and by changing their root architecture (López-Bucio et al. 2003). Their plant root exudates can stimulate various biogeochemical processes to increase the bioavailability of nutrients, known as 'nutrient mining' (Lambers et al. 2008). For example, terrestrial plants in phosphorus-poor soils can access nutrients which were previously insoluble (Lambers et al. 2008) and seagrass in tropical oligotrophic carbonated environments can unbind nutrients from previously inaccessible complexes (Broderson et al. 2017). Also, plant symbionts such as fauna (e.g. Peterson & Heck 1999), mycorrhiza (e.g. Lambers et al. 2008) and other microbes (e.g. Marschner 2007) can increase plant nutrient supply.

1.8. Infauna and the sediment nutrient pool

Located around the roots and rhizomes of aquatic plants, infauna have the potential to affect the nutrient supply to the aquatic plants. Indeed, semi-infaunal, suspension-feeding mussels can supply seagrass with nutrients, and enhance their biomass production (Peterson & Heck 1999, 2001). In soft sediments of the northern Baltic Sea, including sediments within aquatic plant meadows, the bivalve *Limecola balthica* is one of the most prevalent macroinvertebrate infauna species (Rumohr et al. 1996). They are typically found 0-4cm deep in the sediment and, as biodiffusers, they move particles around them in a random manner and over

short distances (Michaud et al. 2005). Their activity, and the activity of their microbial symbionts enrich the sediment with organic carbon, inorganic carbon, methane, oxygen and various other nutrients (Ebenhöh et al. 1995, Michaud et al. 2005, Braeckman et al. 2010, Bonaglia et al. 2017). This activity likely affects the sediment nutrient environment for aquatic plants. Therefore, *L. balthica* could potentially affect plant trait-productivity relationships and thus, which plant growth strategies produce the most biomass. However, we do not know how infauna affect trait-productivity relationships for submerged aquatic plants.

1.9. Environmental factors affecting trait-productivity relationships

The different plant strategies, and thus functional traits, which are related to plant nutrient uptake can vary depending on the sediment nutrient environment (Aerts 1999, Lambers et al. 2008). Likewise, terrestrial plant community functional diversity can vary with sediment nutrient availability (Lambers et al. 2011). We do not yet fully understand the role of aquatic plant traits, strategies and functional diversity for sediment porewater nutrient uptake by temperate aquatic plants. Also, we do not know their implications to the relationship between plant nutrient uptake traits and plant biomass production. It is likely that the relationship between uptake traits and biomass production varies depending on the relative availability of other resources (Udy & Dennison 1997, Touchette & Burkholder 2001). For instance, eutrophication and depth influence light availability (Arthaud et al. 2012, Fu et al. 2014), thus they might lead to different trait-productivity relationships (Fu et al. 2014). It is important to investigate plant resource trade-offs, such as between nutrient supply and light penetration, to better understand the ecology of temperate aquatic plants.

1.10. Submerged aquatic plant meadows in the northern Baltic Sea

The northern Baltic Sea has brackish-water conditions, which means that marine, brackish and limnic plant species coincide within the same meadow (Kautsky 1988, Figure 2). These species

have highly contrasting morphological (Kautsky 1988), physiological (e.g. Gustafsson & Norkko 2016) and life strategy (Kautsky 1988) trait values. These differences in trait values provide a unique opportunity for plant functional trait and functional diversity transplant experiments to be conducted in natural conditions.

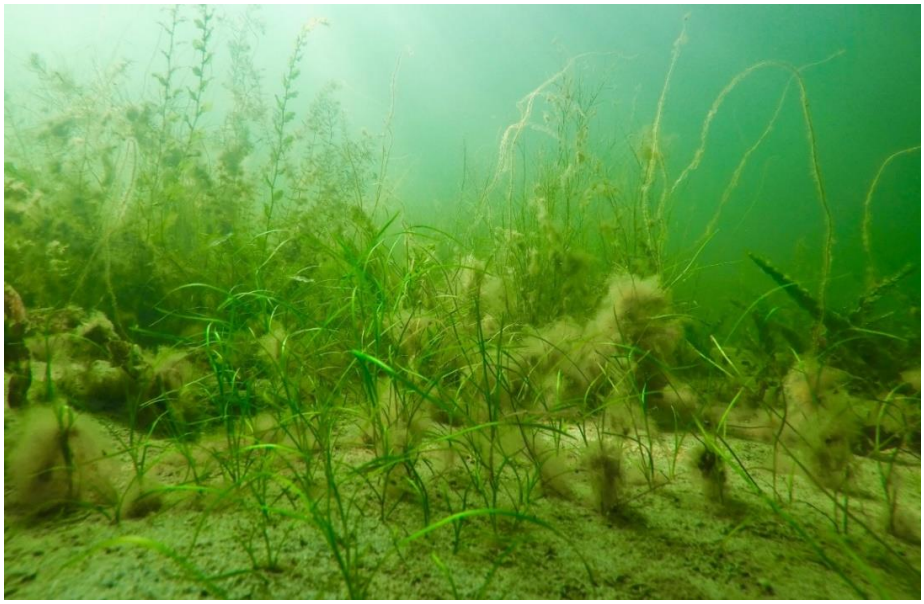

Figure 2. Natural mixed species submerged aquatic plant meadow in the northern Baltic Sea during the growth season, ca. 2.5m deep. Image credit Alf Norkko.

2. AIM OF THESIS

The overall aim of my thesis was to investigate plant functional trait-productivity relationships to better understand plant biomass responses to the environment (Figure 2). It focuses on morphological and chemical plant traits related to the acquisition of nutrients and light. It applies functional traits to investigate trait diversity (functional diversity) and trait regimes (growth strategy) in relation to biomass production. The aims and objectives of each chapter were:

- The aim of Chapter I was to investigate the relationships between plant traits, sediment porewater nitrogen availability and nitrogen uptake rates by individual plant shoots (Figure 3), which was investigated by conducting a short-term enrichment experiment *in situ*.
- Chapter II aimed to investigate the relationship between functional traits, functional diversity indices and plant biomass production (Figure 3). This was achieved by conducting a functional diversity transplant experiment.
- Chapter III aimed to investigate whether the infaunal bivalve *L. balthica* affected the relationships between plant traits, growth strategies and biomass production (Figure 3). For this chapter, the abundance of infauna *L. balthica* was increased in a transplant experiment with mixed plant species.

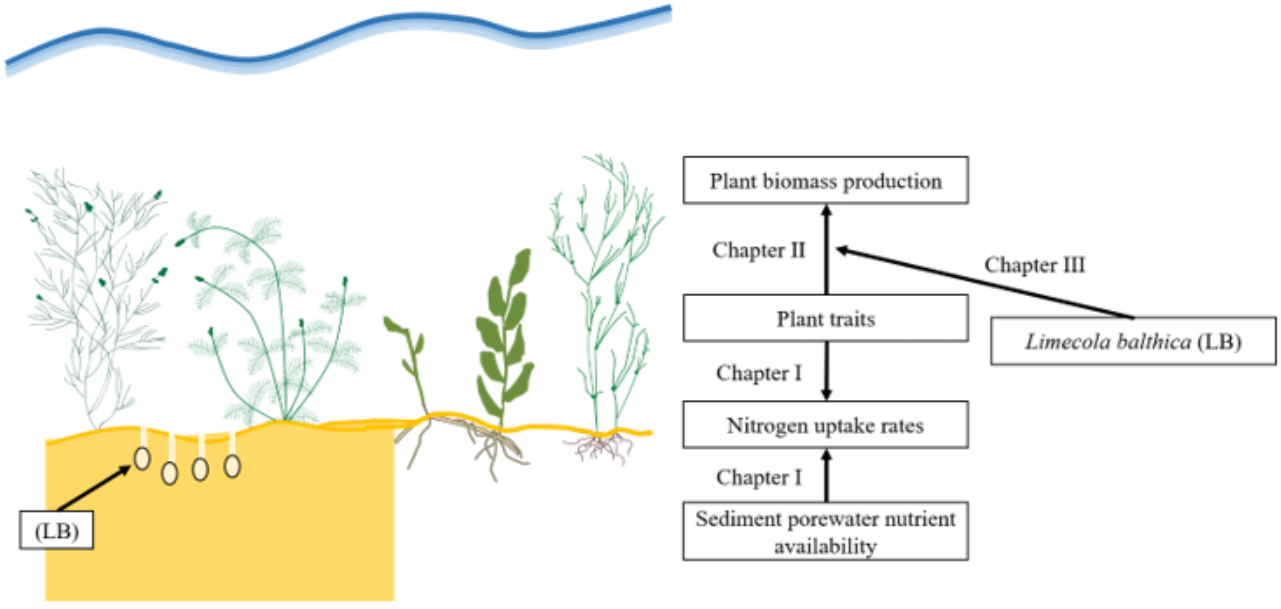

Figure 3. Conceptual diagram showing the relationship between studies for this thesis. Plant graphics courtesy of the Integration and Application Network (ian.umces.edu), University of Maryland Center for Environmental Science. Sources, from left to right: plants 1-2; Tracey Saxby (IAN), plant 3; Dieter Tracey (Marine Botany UQ) and plant 4; Tracey Saxby.

3. METHODS

3.1. Study area and field experiments

This thesis constitutes findings from field experiments conducted *in situ* using SCUBA diving in the northern Baltic Sea (e.g. Salo et al. 2009, Gustafsson & Boström 2011, Salo & Gustafsson 2016). All field work was conducted in shallow, submerged (2–4m) mixed species vegetative communities on the Hanko Peninsula of the Finnish archipelago, northern Baltic Sea. The nutrient enrichment experiment for Chapter I was conducted in the plant communities around Tvärminne Zoological Station, Finland (59° 50′ 400“ N, 23° 14’ 56” E WGS84) while the transplant experiments for Chapters II and III were conducted in a semi-exposed lagoon (Kyan, 59.827415, 23.209903 WGS). Several species were studied in each experiment, and the selection of species was based on their prevalence in the local area and to enhance the variability of traits which they manifested. The species from freshwater origins were *Myriophyllum spicatum*, *Stuckenia pectinata*, *Potamogeton perfoliatus*, *Zannichellia major* and the marine/brackish species were *Ruppia cirrhosa* and *Zostera marina*. An additional freshwater species, *Ceratophyllum demersum*¸ was included in the nutrient enrichment experiment.

3.2. Enrichment experiment (Chapter I)

Incubations were conducted *in situ* for single shoots of plants, or multiple shoots for smaller species (*R. cirrhosa* and *Z. major*). These shoots were located amongst sparse stands of plants and they were at least 1m apart from each other. The height of each shoot did not exceed 20 cm. First, a core (Ø 16 cm, length 20cm) was inserted 16cm into the sediment surrounding a plant shoot. Then, before enrichment, porewater samplers collected depth-integrated water samples in the upper 10 cm of sediment to estimate sediment nutrient availability. Afterwards, the sediment next to each shoot was enriched with 40ml ^{15}N - labelled ammonium sulfate solution (47 µM, 99 at-%) at 7 – 8 cm deep using syringes with extension

tubes. The enrichment was completed during the late morning, so that they would incubate throughout midday. 3.5 hours after enrichment their entire biomass was harvested.

At least 3 replicates were incubated for each species. A further 3 individuals of each species were collected from the surrounding environment to represent the ambient $\delta^{15}N$ and N (% DW) concentrations in tissues. Overall, 9 incubations were conducted each day, and in total 36 incubations were completed (Table 2 in Chapter I). These incubations were conducted during the late growth season of 2015 (August-September). 10 further incubations were conducted in September 2016 for two species; *M. spicatum* and *P. perfoliatus* (Table 2 in Chapter I).

3.3. Functional trait transplant (Chapters II – III)

The plant communities experimental design was identical for Chapters II and III. Bare patches of sand amongst a naturally occurring meadow were the zones for transplanting experimental communities. Before the experiment, they were cleared of lone shoots and buried rhizomes. Experimental zones were 6 bare patch grids (size 8 * 4m) each containing 6 experimental plots at least 1 metre apart from each other. 3 of these experimental plot locations in each patch were for the Chapter II experiment while the further 3 were for Chapter III.

Plants were collected from a natural meadow next to experimental patches and assembled into experimental triculture communities using a random number generator. The species assembly of all communities was identical for Chapters II and III. 8 individuals of each species were assembled onto 30*30 cm plastic grids in random assemblies using cable ties (total 24 shoots). Overall, 18 experimental communities were assembled for each of Chapters II and III (total 36 communities). The communities were carefully transplanted to their experimental locations and the grids were secured into the sand using two stainless steel hooks. The experiment commenced shortly after the growth season began (01/06/2016). The experimental communities at the start of the experiment were standardised by approximate species biomass

using 10 individuals of each species subsampled at the start of the experiment. The survival of communities after transplanting were checked approximately 2 weeks after the experiment commenced. While most transplants were successful the starting biomass was corrected if an individual was lost. All vegetative biomass from the experimental communities was harvested after 15 weeks (14/09/2016). During the experimental period, the daily maximum temperature varied between 9.1 and 19.6 °C ($\bar{x}$ = 15.3 °C) and the daily maximum PAR ranged from 168 to 555 μmol m^{-2} s^{-1} ($\bar{x}$ = 419 μmol m^{-2} s^{-1}). More details about their measurement are described in Chapter II.

3.4. Infauna transplant (Chapter III)

Limecola balthica were experimentally added to 18 transplanted communities using a mark-recapture approach. Approximately 300 *L. balthica* individuals were collected from sediments at the experimental site (5-20 mm valve length), then their valves were marked using non-toxic cosmetic red nail polish. They were monitored in aquarium conditions after being marked and before being transplanted to experimental communities. Those which reburied themselves into sediment after being marked were used for the experimental communities. 10 *L. balthica* individuals were added to the centre of experimental plot for Chapter III on 21/06/2016. After their addition, the communities were left to grow for a further 12 weeks until all biomass was harvested on 14/09/2016. *L. balthica* was collected from the sediment and on average, 5 to 6 out of the 10 original individuals were retrieved. The recaptured *L. balthica* were suspended in an aquarium with filtered seawater overnight inside of nylon bags before they were frozen (-18°C) for future processing.

3.5. Measurement of traits and processes

For the enrichment experiment, it was imperative to process the plants as quickly as possible to prevent the $\delta^{15}N$-labelled fertiliser from leaving the plants before they were oven-dried. Therefore, few traits were measured to optimise processing time. These traits were tissue nitrogen concentrations, $\delta^{15}N$ concentrations, and dry

biomass weights for roots, rhizomes and aboveground parts. Nitrogen uptake response rates (RR) were calculated to estimate the amount of nitrogen plants absorbed from the enriched source. Then, a mass-balance based calculation was used to calculate overall nitrogen uptake rates (UR), which included nitrogen uptake from the non-enriched sediment nutrient source. A detailed description of their measurement is described in Chapter I.

A large suite of plant functional traits was measured for Chapters II and III, which comprised of traits which were potentially related to biomass production. These were median height (cm), leaf area (mm^2), median maximum root length (MMRL, mm), specific root length (SRL), leaf tissue elemental N concentration (% DW), leaf C:N ratios and leaf tissue $\delta^{13}C$ & $\delta^{15}N$ isotope ratios. More details about their measurement, including an informative table, can be found in Chapter II.

L. balthica traits were measured; these traits were valve length (mm) and soft tissue biomass (wet weight [WW], mg), then a condition index ratio (soft tissue biomass [WW, mg]/ valve length [mm]) (e.g. Duquesne et al. 2004).

3.6. Functional diversity calculations

Functional diversity indices were calculated for Chapter II. First, Spearman's Rank correlation was used to check for significant relationships between traits using a False Discovery Rate (Benjamini & Hochberg 1995) to reduce the likelihood of Type I errors. Leaf area was strongly correlated to plant height (Chapter II) therefore leaf area was removed from these calculations. The remaining traits were median height (cm), median maximum root length (MMRL, mm), specific root length (SRL), leaf tissue elemental N concentrations (% DW), and leaf tissue $\delta^{13}C$ & $\delta^{15}N$ isotope ratios. Functional diversity indices were then calculated using the "FD" package (Laliberté et al. 2014). The indices were Functional Richness (FRic), Functional Evenness (FEve) and Functional Divergence (FDiv) (Laliberté & Legendre 2010, Mouchet et al. 2010, Schleuter et al. 2010). FRic quantifies the volume of functional space which the traits occupy, FEve describes the

regularity of the distribution of mean species traits within the trait space for a community, while FDiv describes the position of species' trait clusters within the trait space (Mason et al. 2005, Villéger et al. 2008, Laliberté & Legendre 2010, Schleuter et al. 2010). The estimates for these indices were improved by weighting different traits by their estimated importance for productivity (see Petchey & Gaston 2006). This study used trait-productivity relationships previously collected by a spatial survey conducted in the same region (Gustafsson & Norkko 2019). When traits were significantly important for primary production across communities in the spatial survey, standardised versions of their coefficient estimates were used to represent their relative weights for functional diversity indices (Height = 33, $\delta^{15}N$ = 13, $\delta^{13}C$ = 11) (Petchey & Gaston 2006). Traits which were not significantly linked to productivity across communities in the spatial survey were weighted as 1.

3.7. Statistical analyses

For all experiments, statistical analyses were conducted using R (R Core Team 2018) and the main types of data analyses were generalised linear models, correlation analyses and quantile regression analyses. Quantile regression analyses, otherwise known as 'factor ceiling' analyses, are used to explore the maximum effect that a factor has on a variable (Thomson et al. 1996, Thrush et al. 2003)

For Chapter I, 95th quantile regression analyses were used to estimate the relationship between plant biomass and N uptake rates (UR & RR, $\mu gN\ gN^{-1}\ h^{-1}$), leaf tissue N concentrations (% DW) and sediment porewater NH_4^+ availability (µM). Then, a multiple-regression style General Linear Model (GLM) was used to analyse how uptake rates (UR & RR) were affected by species identity and sediment porewater NH_4^+ availability. For this analysis, 3 replicates of each species were randomly selected from 2015 data for equal group sizes. *Ceratophyllum demersum* was not included in this analysis because it did not have true roots and another species (*Zannichellia major*) was removed due to replicate loss. Following this analysis, there was a final regression analysis between uptake

rates (RR, UR) and root trait data from previously collected data (Specific root length and median maximum root length, Gustafsson & Norkko 2019). Such analyses were an approximate exploration for potential effects of root traits to uptake rates.

For Chapter II, the relationship between functional diversity indices (FRic, FEve & FDiv) and biomass production were evaluated using linear regression analyses. Following this, the relationships between traits and biomass production were assessed using many linear regressions and a permutation-based multiple-regression style GLM which included a backwards-step selection process. The relationship between leaf tissue $\delta^{13}C$ and biomass production was further examines using a generalised linear model to test for species identity influence to its relationship with biomass production. Similarly, C:N relationships to productivity were examined to test for species effects using factor ceiling analysis.

For Chapter III, part of the analysis was very similar to Chapter II. However, instead of exploring functional diversity indices it investigated the relationship between *L. balthica* condition index and plant community leaf tissue nitrogen concentrations (% DW) and isotope ratios ($\delta^{13}C$, $\delta^{15}N$) using linear regressions. A T-test was used to compare total experimental biomass production between Chapters II and II. Then, the relationships between traits and biomass production were assessed using many linear regressions. These relationships were summarised in a permutation-based multiple-regression style GLM with a backwards-step selection process. The relationship between Specific Root Length (SRL: Root thickness/density) and biomass production was explored further using a Generalised Least Squares model for SRL of each species in each community. Amongst routine quality control checks, we tested for multicollinearity using Variance Inflation Factors (VIF). Then SRL was compared to different types of biomass for each species in each community (aboveground biomass, belowground biomass, shoot frequency) using a GLM. Plant trait-productivity relationships and mean trait CWMs were compared between Chapters II and II using generalised

linear models, a non-parametric MANOVA-style test and multiple T-test comparisons.

4. RESULTS AND DISCUSSION

Chapter I parameterised plant biomass factors which can affect sediment nutrient availability, nitrogen uptake and nitrogen storage by plants. Larger plants were less likely to reach uptake rates as high as smaller plants, and they were more likely to have NH_4^+ -depleted sediment porewater concentrations in the adjacent sediment. Overall, plants exhibited biomass-demand driven nitrogen uptake rates, and aboveground tissue N concentrations (% DW) of larger plants were less likely to reach the same concentrations smaller plants. Therefore, Chapter I identified that plant biomass potentially affects sediment porewater NH_4^+ availability, as well as sediment nitrogen uptake. It also identified possible unfulfilled potential of nutrient cycling by larger plants in temperate submerged environments. Based on findings of Chapter I, it was hypothesised that plant traits or infauna, which might increase access to new nutrient sources, could benefit plant biomass production. Chapter II showed that aquatic plant functional diversity was related to community productivity likely by selecting for traits which increased community light capture (selection effect). It also identified that carbon supply might not have been replete for productive plant communities. However, despite this and findings from Chapter I, sediment nutrient uptake traits were not significantly related to productivity. Height had a disproportionately large effect to community productivity because it likely enhanced biomass production by a competitive height interaction between species in a community. Chapter III, which had similar experimental design to Chapter II with *L. balthica* additions, exhibited highly contrasting trait-productivity relationships to Chapter II. A different growth strategy was most closely related to community productivity, because height was not related to productivity but instead Specific Root Length (SRL) was most strongly related to community productivity. SRL was related to community shoot frequency. Both SRL and shoot frequency represent strategies to invest in absorbing nutrients from the sediment nutrient source. Therefore, productive communities were

those which had growth strategies characterising investment of nutrient absorption from the sediment. Relationships between plant leaf nutrient concentrations, isotopic ratios and *L. balthica* condition indices suggested that *L. balthica* had enriched plant communities with nutrients. Overall, Chapter III showed that infauna can change plant functional trait-productivity relationships and the biomass production of different plant community growth strategies.

4.1. Chapter I: Nitrogen uptake rates from the sediment porewater

This study aimed to investigate sediment porewater nitrogen uptake efficiency by individual plant shoots and to explore which traits increased uptake rates. This was achieved using a short-term nutrient enrichment experiment of single shoots of several plant species *in situ*. Its main findings related to the natural variability of sediment porewater NH_4^+ concentrations, and the relationships between plant biomass, uptake rates and sediment porewater NH_4^+ concentrations. Background NH_4^+ concentrations of sediment porewater were highly variable between individual plants. Plant species identity did not significantly affect nitrogen uptake rates. Relationships between sediment porewater NH_4^+ concentrations and nitrogen uptake rates were unexpectedly weak. Instead, there was a significant logarithmic decline in the 95^{th} quantile of nitrogen uptake rates with increasing plant shoot biomass (Figure 4). Likewise, sediment NH_4^+ concentrations and plant aboveground tissue N (% DW) exhibited similar relationships to plant shoot biomass (Figure 4). Comparisons to previously collected data (Gustafsson & Norkko 2019) indicated that uptake rates could potentially increase for species with increased root length (Chapter I).

Larger plants would have needed to absorb more nitrogen to achieve the same leaf tissue nitrogen concentrations and uptake rates as smaller plants (hereafter biomass-driven nutrient demand). Therefore, the larger plants were unable to reach the same uptake rates as smaller plants. The larger plants were more

likely to have depleted NH_4^+ from the surrounding sediment nutrient pool.

Overall, Chapter I parameterised plant biomass factors which can affect sediment nutrient availability, and nitrogen uptake and storage by plants. It has highlighted the potential importance of root traits, e.g. Root length, for submerged aquatic plants to access new nutrient pools. From a generalised perspective, results from Chapter I showed that temperate aquatic plants might not necessarily have replete nutrient sources, even though one of their greatest ecosystem threats is eutrophication (Andersen et al. 2009, Gustafsson et al. 2012). This builds on previous evidence which shows seagrass can produce more biomass in response to nutrient enrichment so long as there are not larger-scale ecosystem effects which become deleterious to plant growth (Cabaço et al. 2013).

The following chapters of this thesis are valuable to investigate questions which arise from Chapter I. For example, whether plant communities which manifested increased root length would have higher community productivity and whether communities would be more productive if there were increased frequencies of infauna.

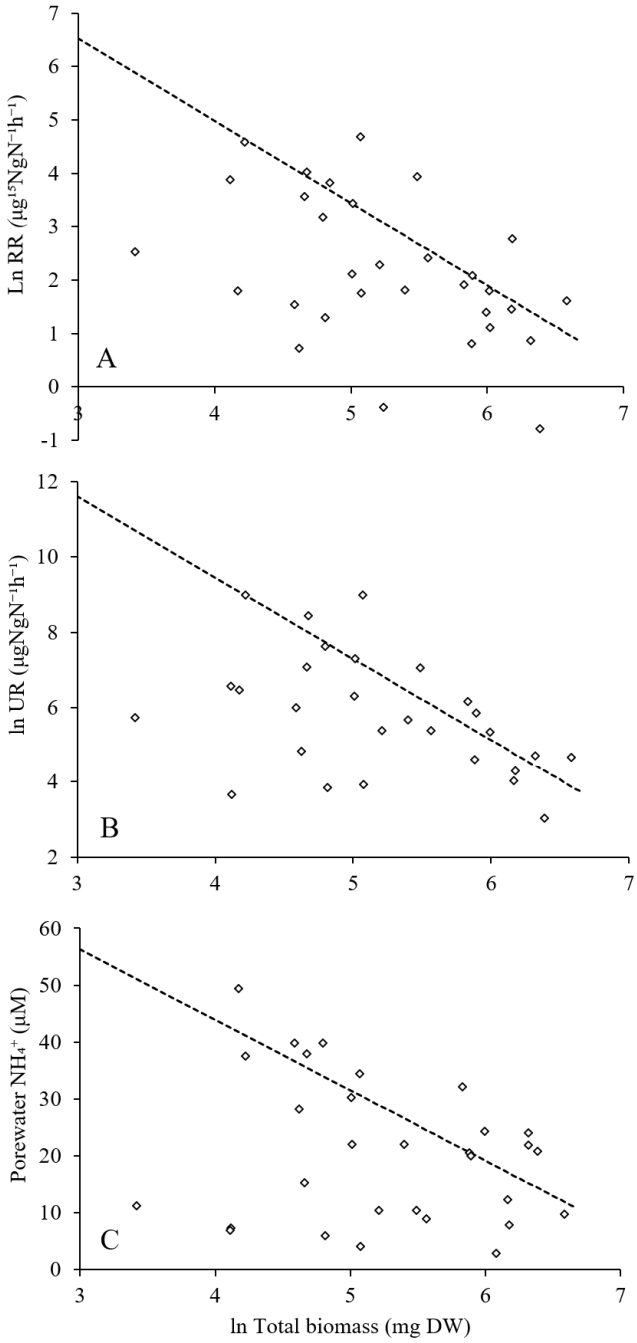

Figure 4. Total plant biomass (mg Dry Weight, DW) with, A: N uptake response rates (RR, ln-transformed, µgN gN^{-1} h^{-1}), n = 29, B: N uptake rates (UR, ln (*V* + 1), µgN gN^{-1} h^{-1}), n = 28, C: Porewater ammonium NH_4^+ concentrations (µM), n = 30. Dotted lines show 95th percentiles.

4.2. Chapter II: Plant functional traits and functional diversity effects to productivity

The aim of Chapter II was to investigate the role of plant functional traits and functional diversity for plant community productivity. This was achieved by conducting a 15-week transplant experiment *in situ*. Species composition was manipulated in experimental triculture plant communities to change the variability of plant traits and test their effect to community biomass production. Species manipulations had affected community productivity greatly, because community productivity varied by more than four times across treatments. Functional richness was significantly related to community productivity (Figure 5), while functional evenness and functional divergence were not. Height, leaf area and leaf tissue $\delta^{13}C$ were significantly related to community productivity (Figures 6-8). There was a significant relationship between community height range and community productivity (Figure 6B) and this was caused by variability of the height of the tallest species rather than the height of the shortest species. The height of the tallest species was significantly correlated to the height of the second tallest species (Figure 6C).

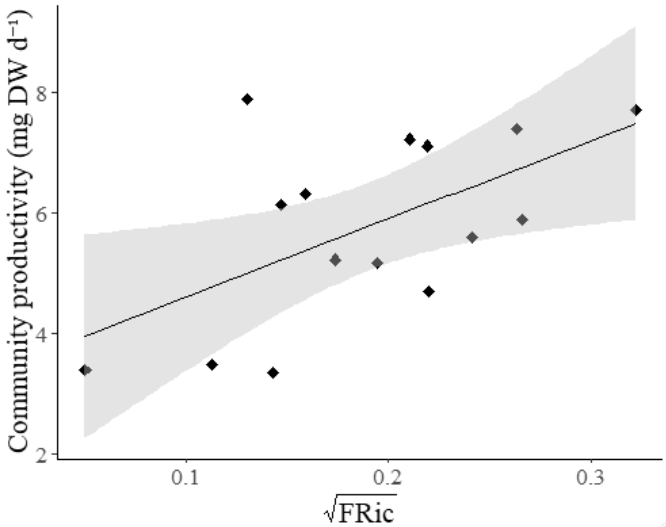

Figure 5. Relationship between Functional Richness (FRic, square root transformed) and community productivity (mg DW d^{-1}). Solid line: Line of best fit, shaded area: 95% confidence intervals, n = 15.

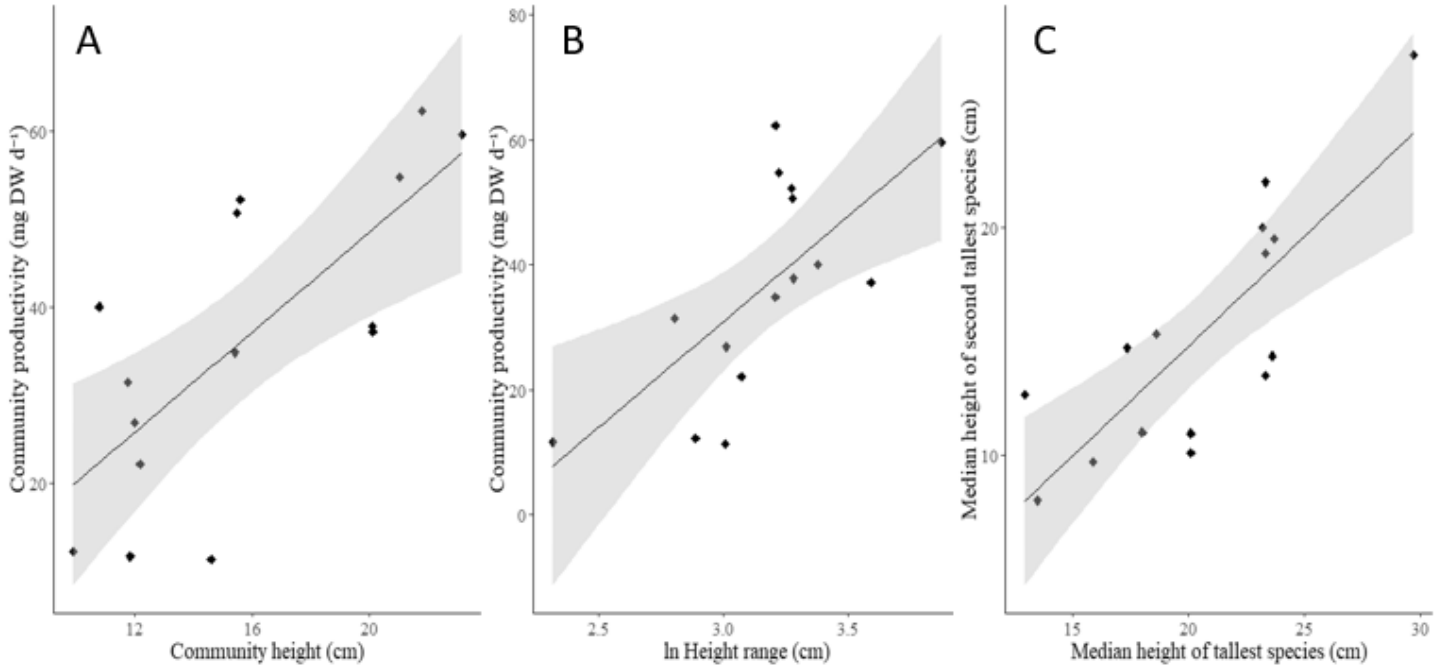

Figure 6. Relationship between A. Community height (cm) and community productivity (mg DW d^{-1}), n = 14, B. Community height range (ln-transformed, cm) and community productivity (mg DW d^{-1}), n = 14, C. Median height of tallest species (cm) and median height of second tallest species (cm), n = 14. Solid line: Line of best fit, shaded area: 95% confidence intervals.

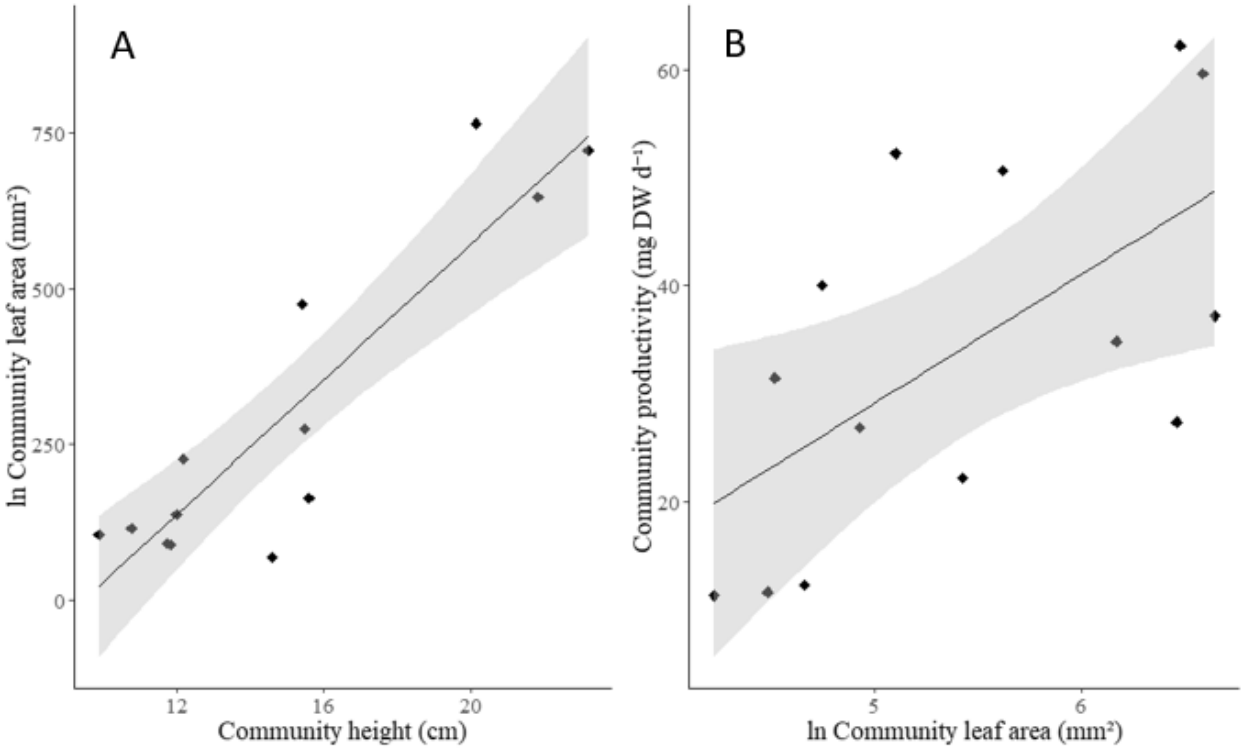

Figure 7. Relationship between A. Community height (cm) and community leaf area (ln-transformed, mm²), n = 13, B. Community leaf area (ln-transformed, mm²) and community productivity (mg DW d^{-1}), n = 13. Solid line: Line of best fit, shaded area: 95% confidence intervals.

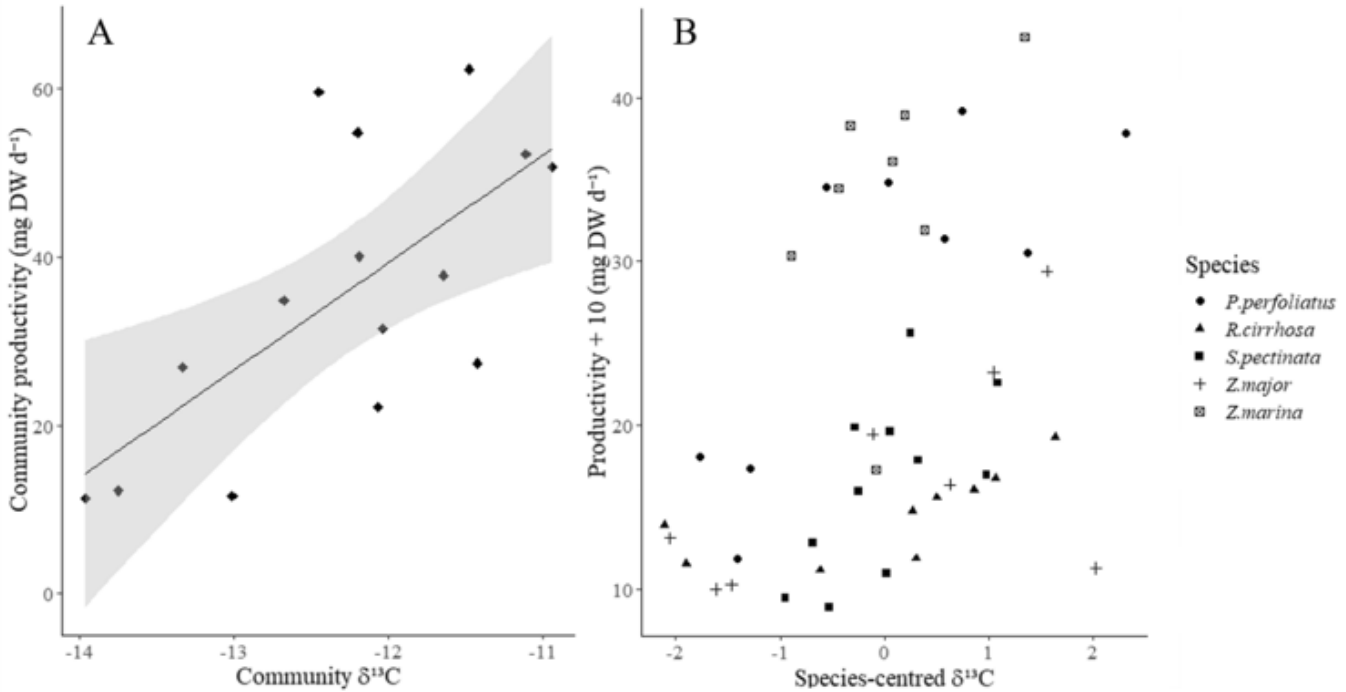

Figure 8. A. Relationship between community leaf tissue $\delta^{13}C$ and community productivity (mg DW d^{-1}); solid line: Line of best fit, shaded area: 95% confidence intervals, n = 14. B. Relationship between species-centred leaf tissue $\delta^{13}C$ of each species in each community and their productivity, n = 44 (+10 in accordance to its entry in a generalised linear model with error family Gamma, mg DW d^{-1}).

The relationship between functional richness and productivity was most likely owing to the presence of taller individuals (selection effect; Loreau & Hector 2001) because height was weighted heavily in its calculation and community height range was significantly related to biomass production. Results supported previous evidence that plant height is closely related to plant biomass production in submerged aquatic plant communities (Figure 6, Díaz et al. 2004, Gustafsson & Norkko 2019). It also identified that leaf area was closely related to productivity (Figures 7). Both height and leaf area characterise plant size and light capture. This experiment identified that height could have had a disproportionately high effect to biomass production because it stimulated communities to produce more biomass during competitive interactions amongst species (Figure 6C, Hector et al. 1999). However, the effects of height and leaf area to biomass production could not be evaluated separately because they were correlated (Figure 7A). Biomass production likely had a consequence to carbon supply (Hu et al. 2012, Buapet et al. 2013, Chapter II), because plants became significantly enriched with the heavier isotope $\delta^{13}C$ with increasing productivity (Figure 8). However, changes in plant species identity were partly responsible for this relationship. This study supported results from a previous survey of an aquatic plant meadow which suggested that plant functional traits are more descriptive for productivity compared to functional diversity indices (Fu et al. 2014).

Overall, Chapter II concluded that functional diversity was significantly related to primary productivity likely by selecting for traits which enhanced light capture. Also, high plant biomass production likely had consequences for plant carbon supply. Chapter II results build from results of Chapter I because they show that while plant nutrient supply might not be replete, morphological root traits were not significantly related to biomass production. It is valuable that the next chapter investigates whether the relationship between plant traits and biomass production remained consistent when the density of the infaunal bivalve *L.*

balthica increased. Indeed, perhaps *L. balthica* could have affected the nutrient supply to the plants.

4.3. Chapter III: Infauna effects to plant functional trait-productivity relationships

Chapter III aimed to provide a holistic understanding of submerged aquatic plant community by investigating the effects of a common infauna species to plant trait-productivity relationships. This was achieved by a similar experimental design to Chapter II with additions of 10 *L. balthica* individuals to each plot using a mark-recapture technique. Overall, *L. balthica* individuals had not affected total experimental biomass production because there was no significant difference in total experimental plant biomass between experiments from Chapters II and III. Community productivity was related to Specific Root Length (SRL) and leaf area, and there was a marginally non-significant relationship between community productivity and median maximum root length (MMRL). Of all traits measured, SRL was most strongly related to productivity (Figure 9). There was collinearity between SRL and species identity, therefore SRL could not be interpreted separately to other species traits which could have coincided. Communities with lower SRL were significantly more likely to have higher shoot frequency. There was a marginally non-significant relationship between SRL and belowground biomass. Interestingly, SRL was not significantly related to aboveground biomass production. There were relationships between *L. balthica* condition index and leaf tissue N (% DW), $\delta^{15}N$ and $\delta^{13}C$.

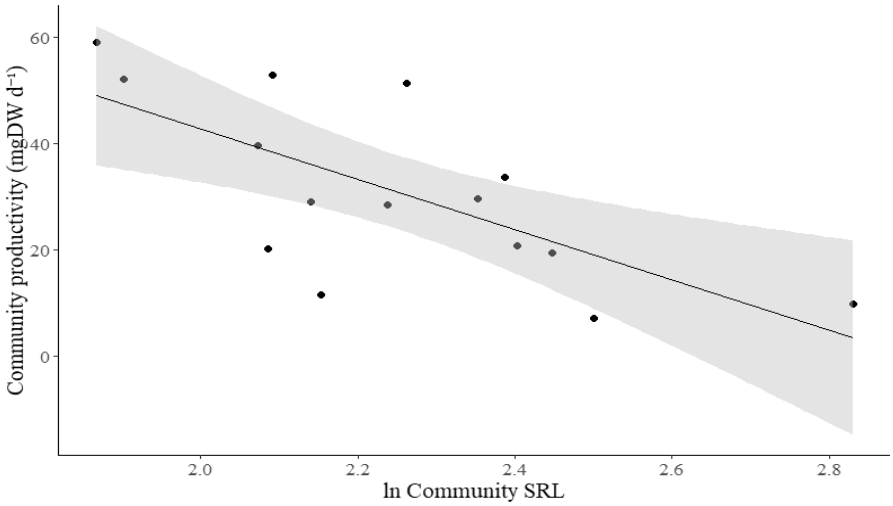

Figure 9. Relationship between community Specific Root Length (SRL, ln-transformed) and community productivity (mg DW d^{-1}), n = 15. Solid line: Line of best fit, shaded area: 95% confidence intervals.

SRL represents the thickness or density of roots (Perez-Harguindeguy et al. 2013). The SRL of each species in each community was related to species-level shoot frequency, and shoot proliferation represents a strategy for utilising sediment nutrient sources (Campbell et al. 1991, de Kroon & Mommer 2006, Kembel et al. 2008, Furman et al. 2017). Therefore, the most productive communities manifested traits which were investments into absorbing nutrients from the sediment nutrient source. It is notable that there were not relationships between community height and community productivity because height is conventionally strongly related to community productivity (Chapter II). The relationships between plant leaf tissue nutrient concentrations and *L. balthica* condition indices suggested that it was highly likely that *L. balthica* increased sediment nutrient mobility and enriched the plants with nutrients (see Chapter II for isotope-specific inferences). Also, unlike results from Chapter II, plant community leaf tissue $\delta^{13}C$ was not linked to community biomass production. This indicated there might not have been depleted sources of C in communities with *L. balthica* additions, perhaps *L. balthica* had enriched plants

with carbon. Nevertheless, species identity could have been partly responsible for this relationship as observed in Chapter II.

Overall, Chapter III found that infauna, common in aquatic plant meadows, can change aquatic plant trait-productivity relationships and biomass production of different plant growth strategies.

5. IMPLICATIONS AND OPPORTUNITIES FOR FURTHER STUDY

5.1. Baltic Sea plant ecology at a global scale

Submerged aquatic plant meadows in the northern Baltic Sea can have a relatively high species diversity because the brackish water conditions allow marine, estuarine and limnic species to coincide within the same meadow (Kautsky 1988). Other submerged aquatic plant meadows with potentially high species diversity within a single meadow include freshwater meadows (Arthaud et al. 2013, Murphy et al. 2019), brackish-water bodies (Kautsky 1988, Murphy et al. 2019) and seagrass meadows in the Tropical IndoPacific seagrass bioregion (Short et al. 2007). By examining mixed-species communities in the Baltic Sea, it has been possible to use the naturally occurring plant functional trait variability within meadows to investigate relationships between plant traits and ecosystem processes. Such investigations in this thesis would have been highly difficult to conduct in monoculture meadows, e.g. most seagrass meadows in the North Atlantic temperate seagrass bioregion (Short et al. 2007). Therefore, the natural variability in plant functional traits of mixed species communities in the Baltic Sea are valuable assets to further understand functioning of submerged temperate aquatic plants.

The collective understanding gained from this thesis can potentially be applied to temperate monoculture meadows, because the temperate soft-sediment environments of Baltic Sea plant meadows are arguably relatable to other temperate aquatic plant environments (e.g. Short et al. 2007). Also, there is relatability in the understanding gained from this thesis because its findings are comparable to previous functional diversity surveys conducted in freshwater plant communities (e.g. Fu et al. 2014). Furthermore, aspects of mixed-community plant ecology can be tested in monocultures using alternative approaches to investigating species trait-process relationships. For example, Furman et al. (2017)

investigated seagrass monoculture shoot proliferation response to sediment nutrient enrichment and its findings were highly complementary to findings from this thesis (Chapters I & III). They found that *Zostera marina* meadows can actively forage for nutrients by proliferating shoots into areas of higher sediment nutrient availability. These findings are relatable to Chapter I because both studies illustrated the potential sediment nutrient demand by temperate submerged aquatic plants. Because, Chapter I showed that increased plant shoot biomass is linked to potential decreased sediment NH_4^+ availability and Furman et al. (2017) showed that seagrass can proliferate shoots into areas of higher sediment nutrient availability to enhance their access to sediment nutrient sources. Chapter III further built from these insights because infauna additions had highly likely changed sediment nutrient conditions, and its results showed that plant functional trait-productivity relationships were different with this likely change in the sediment. This example illustrates how findings from this thesis can be tentatively applied to monocultures. Therefore, the generalisability of results can be extended much further than Baltic mixed species meadows.

It is likely necessary to conduct further investigations into the relationships between plant traits and ecosystem processes in different temperate environments to account for variability environmental factors which could affect trait-process relationships, e.g. Sediment type (Erftemeijer & Middelburg 1993, Short et al. 1990). Another aspect to explore is connectivity to other habitats such as oyster beds, kelp forests and mussel reefs. The experiments of this thesis relied heavily on the natural trait variability which occur within mixed species meadows, therefore understandably they are unlikely effective approaches for investigations within meadows with low species diversity. However, for meadows with low species diversity it would be valuable to advance research using an interdisciplinary approach which incorporates aspects of plant functional trait ecology and other fields such as habitat connectivity (Bornette et al. 1988, Berckström et al. 2013) and sediment biogeochemistry (e.g. Erftemeijer &

Middelberg 1993). For example, an experiment which measures functional trait response and shoot proliferation to sediment nutrient enrichment or infauna additions in different sediment types and in seagrass meadows with different amounts of connectivity to other ecosystems (e.g. Mussel reefs).

Experimental approaches of this thesis could be repeated in other mixed species aquatic plant meadows in different ecosystems. For example, the Tropical Indo-Pacific seagrass bioregion has the highest species diversity of seagrass in the world with up to 14 different species coinciding on the same reef flat (Short et al. 2007). In tropical ecosystems such as these, trait-process relationships are likely to be highly contrasting to trait-process relationships in Baltic Sea plant meadows. For example, light attenuation and nutrient toxicity by coastal nutrient runoff is less likely to occur, and more influential factors are likely to include hypersalinity, UV radiation exposure and light attenuation by sediment resuspension (Short et al. 2007, Onuf et al. 2003). By conducting similar experimental approaches to this thesis in different ecosystems, it would enhance the global understanding of aquatic plant biomass responses to environmental factors.

5.2. Environmental factors affect plant functional trait-productivity relationships

Previous evidence shows that multiple environmental factors affect plant biomass responses to changes in a single environmental factor, for example, Udy & Dennison (1997) and Touchette & Burkholder (2001) described the context-dependence of plant biomass responses to sediment nutrient enrichment (Table 1). Such contexts which they describe may also affect trait-productivity relationships. This thesis provides new evidence that ecological interactions between plants and infauna affect plant trait-productivity relationships, most likely by changes in sediment nutrient conditions. Therefore, it is necessary to revise and potentially update the current descriptions of context dependent biomass responses to sediment nutrient enrichment (Table 1). The descriptions should potentially be updated to include changes in

biomass production of different plant growth strategies and the environmental context which would lead to such changes. There are two potential approaches to update the descriptions: Firstly, growth strategy could be incorporated into category II where plants respond to sediment nutrient enrichment physiologically but not with increased biomass production (Table 1). In this category, the plants respond positively to sediment nutrient conditions, but other factors are expected to limit biomass production. Growth strategy can potentially be integrated to this category because it indicates that there is a biomass trade-off with other potentially limiting environmental factors. However, this assumes that other environmental factors are more limiting to aquatic plant growth therefore one would expect plants to invest more biomass in remediating the other limiting environmental factor e.g. increase in aboveground biomass for light capture in response to sediment nutrient enrichment (e.g. Lee & Dunton 2000, Maurer & Zedler 2002, Frazer et al. 2016). However, plant growth strategies in the presence of *L. balthica* additions exhibited the reverse (Chapter III). Given that *L. balthica* had likely enriched the plants with nutrients, it brings rise to question whether plant growth strategy is accurately represented by Category II (Table 1). As a result, a second approach might be more suitable for updating the context-dependent response of aquatic plants to sediment nutrient enrichment: Use previously defined categories (Table 1) as guidance to develop a descriptive flowchart of plant responses to sediment nutrient enrichment (e.g. Figure 10) which replaces previous categories (Udy & Denison 1997, Touchette & Burkholder 2001).

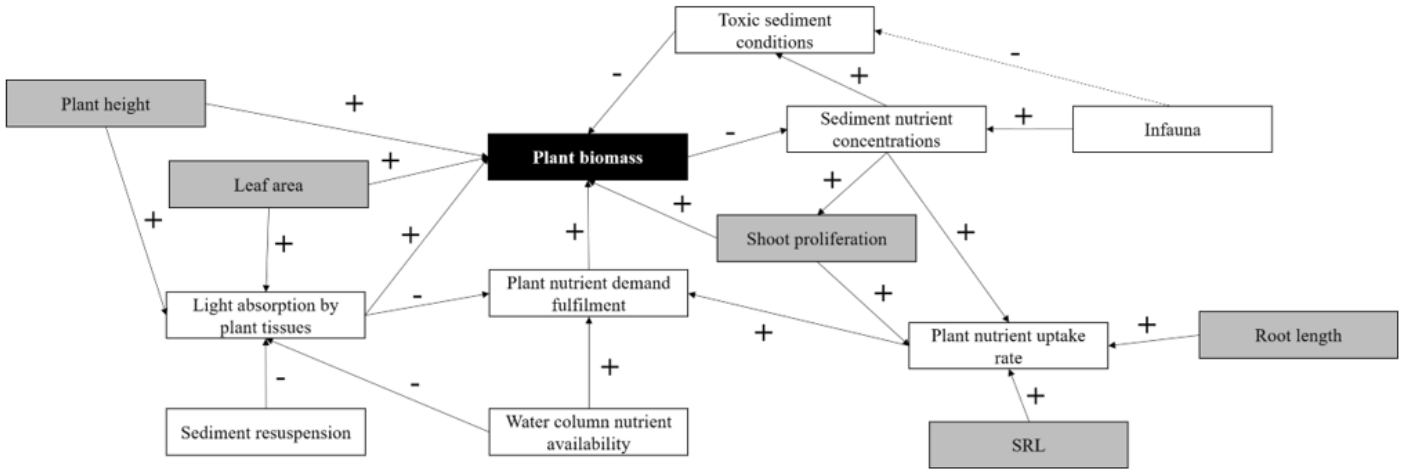

Figure 10. Conceptual diagram as suggested representation of context-dependent plant biomass response to sediment nutrient enrichment. Plant traits in shaded boxes, and plant biomass is in a black box as the central focus of the diagram. Links identified based on results of this thesis and literature cited in thesis summary. Additional link (dotted arrow line) between infauna and direct reduction of toxic sediment conditions by sulphide reduction: Observed for bivalves in the families Lucinidae and Solemyidae (Reynolds et al. 2007, van der Heide et al. 2012).

Before utilising the suggested flowchart (Figure 10), it is necessary to (i) confirm that infauna enrich the sediment nutrient source for aquatic plants. Plant leaf tissue nutrient concentrations in Ch III suggested that *L. balthica* could have enriched the plants with nutrients, and such an interpretation is supported by previous literature (e.g. Peterson & Heck 2001, Gagnon et al. 2020). Therefore, it is possible to continue with moderate confidence that *L. balthica* had indeed enriched the plants with nutrients. Otherwise, it is nonetheless important to account for plant responses to the multiple effects which infauna have to aquatic plants because infauna are common in aquatic plant meadows (Gagnon et al. 2020). Therefore, arguably the flowchart would still be beneficial even if sediment nutrient enrichment was not the only mechanism by which infauna affected plants, and infauna affect submerged aquatic plants by a variety of mechanisms (Gagnon et al. 2020). However, if a link could not be confirmed between infauna and sediment nutrient enrichment then it would be necessary to define the flowchart differently and adjust the flowchart with changes specific to infauna effects rather than sediment nutrient enrichment. The next suggested step to improve the flowchart is to (ii) understand the context of plant community change by species change versus intraspecific trait variation, which can be tested by synthesising data from Chapters II and III then comparing species composition change to trait variability change with *L. balthica* additions. After developing the flowchart, an opportunity for further study would be to empirically test it using structural equation modelling and measurements from natural communities (i.e. Survey data which includes plant trait data, abiotic factors and infauna community data). This would provide an important quantification of plant responses to environmental change and it would improve the understanding of context-dependent plant responses to nutrient enrichment. By doing this, it would also be a noticeable step forwards to increase the accuracy of predictive modelling of plant responses to future change.

5.3. Infauna likely affect plant functional trait-productivity relationships

Infauna are renowned to be prevalent in submerged aquatic plant meadows, and it is important to understand their role for aquatic plant functioning to holistically understand aquatic plant ecology (Naeem 2002, Raffaelli et al. 2002, Duffy 2006). This thesis contributes towards filling this knowledge gap about holistic aquatic plant ecology by providing new evidence that infauna potentially engineer changes in plant trait-productivity relationships and resultantly, plant community growth strategies related to biomass production. An opportunity for further study would be to compare naturally occurring infauna community compositions to plant trait-productivity relationships in an experiment with similar design to Chapters II and III. It would also be valuable to compare plant trait-productivity relationships in different environments with experimental treatments of infauna density increases. This would provide even greater insight and context to understand more fully the effects of infauna to aquatic plant ecosystem functioning.

5.4. Traits which enhance sediment nutrient uptake by aquatic plants

Aerts (1999) discussed how environmental context affected relationships between terrestrial plant traits and nutrient uptake rates from the sediment. For example, terrestrial plants inhabiting nutrient rich soils were more likely to have faster nutrient uptake rates from the sediment if their roots manifested physiological traits which enhanced the uptake kinetics from a localised nutrient source (e.g. High proton pump frequency per unit absorptive root area, Jackson et al. 1990). However, in nutrient poor soils sediment nutrient uptake rates would more likely be related to root traits which increase access to edaphic nutrient sources (e.g. Variability in root length and specific root length). Results from this thesis suggest that temperate submerged aquatic plant traits which increase sediment nutrient uptake would more likely be traits which enhance access to spatio-temporal sediment nutrient sources

(Chapter I). For example, traits such as increased root length and processes like active foraging by root proliferation (Furman et al. 2017) and nutrient translocation between ramets (Marbà et al. 2012, Roiloa and Hutchings 2013). Results from Chapter III support this suggestion because *L. balthica* most likely changed sediment nutrient supply to plants, and plants with *L. balthica* additions had different plant trait-productivity relationships to plant communities without *L. balthica* additions.

The findings of this thesis about plant traits and sediment nutrient uptake rates (Chapter I) could be applied to temperate aquatic plant meadows which do not have dense root-rhizome networks. However, its results may not be ecologically relevant to submerged aquatic plant meadows with dense root-rhizome networks. Indeed, Chapter I showed that there are relationships between plant shoot biomass and NH_4^+ concentrations in the sediment. However, Chapter I was focussed on lone plant shoots amongst sparse stands of plants and these plants did not have dense root-rhizome networks. Therefore, communities which have dense root-rhizome networks could have depleted nutrients from the sediment nutrient source to a greater extent, perhaps to an extreme. Such ecosystems include Mediterranean seagrass, tropical seagrass and other seagrass meadows whose roots and rhizomes form dense 'mattes' (Short et al. 2007). Alcoverro et al. (2000) observed that roots and rhizomes contributed a minor amount to the seasonal nutrient budget of Mediterranean seagrass *Posidonia oceanica*, while the aboveground biomass and nutrient retranslocation participated major roles in the *P. oceanica* nutrient budget. Therefore, as nutrient uptake by *P. oceanica* was likely affected by the relative nutrient availability of the sediment and the water column (Touchette and Burkholder 2000), seagrass would absorb greater relative amounts of nutrients from the water column when the sediment nutrient concentrations are low. Further experimental investigation is needed to test whether increased sediment nutrient availability would change nutrient budgeting for seagrass with dense root-rhizome networks and whether this affects plant functional trait-productivity relationships.

In seagrass ecosystems with dense root-rhizome networks, traits which enhance nutrient absorption from the sediment may not greatly benefit nutrient supply to plants because the sediment may not be a reliable nutrient source (Alcoverro et al. 2000) and the water column could also be a major nutrient source (Erftemeijer & Middelberg 1995). Traits which enhance nutrient supply to aquatic plants might be those which enhance nutrient recycling (Mateo & Romero 1997, LePoint et al. 2002) and nutrient translocation between ramets (Marbà et al. 2012). Also, infauna might participate a different role for aquatic plant nutrient supply compared to their role examined in this thesis. For example, their role as decomposers of decaying organic matter (Koike et al. 1987) may be highly functionally important compared to other functions such as particle transport (e.g. Michaud et al. 2005).

5.5. Aquatic plant growth strategies and the sediment nutrient source

Previous evidence suggested that sediment nutrient enrichment could affect which plant growth strategies are related to productivity, because sediment nutrient enrichment has led to relative changes in aboveground versus belowground biomass production (aboveground: belowground biomass ratios, Lee & Dunton 2000, Maurer & Zedler 2002, Frazer et al. 2016). Results of this thesis fills a knowledge gap by providing insights into biomass production by different plant growth strategies in response to changes in the sediment, particularly changes in sediment conditions by infauna *L. balthica*. In Chapter III, infauna had most likely enriched plant communities with nutrients as observed by plant leaf tissue nutrient concentrations. However, the specific mechanism(s) of nutrient exchange between *L. balthica* and plants have not been empirically demonstrated, because inferences rely on changes in plant leaf tissue nutrient concentrations. It is an established paradigm to use plant leaf tissue nutrient concentrations to indicate relative changes in nutrient availability to plants (e.g. Duarte 1990), however it would be highly valuable to confirm the mechanisms of nutrient exchange between infauna and plants, such as *L. balthica* and Baltic Sea plants. Based on the

findings of this thesis, the most effective approach for identifying the mechanisms of interaction between *L. balthica* and plants would be to conduct isotope-tracing experiments. For example, Evrard et al. (2005) used $\delta^{15}N$ – labelled phytodetritus to confirm that seagrass absorbed nutrients from phytodetritus which can be entrained from the water column. Also, dendrochronologists use compound-specific isotopic analyses to understand physiological pathways within trees (e.g. Rinne et al. 2015), perhaps compound-specific isotopic analyses might also be useful to understand the chemical pathways between infauna and plants. Based on the findings of this thesis, it is not recommended to rely on nutrient flux measurements in the sediment porewater without tracers, because Chapter I showed that the nutrient concentrations in the sediment porewater potentially represent the balance between sediment nutrient supply and nutrient absorption by plants (biomass-driven demand). Therefore, without further confirmation by isotope tracers, net nutrient flux measurements (or e.g. porewater nutrient concentrations) might not represent the true dynamics of the nutrient exchange by making it appear lower than its true value. However, this is highly dependent on the research question and results of this thesis do not undermine the value of nutrient flux and porewater concentration measurements when they are appropriately used.

Community growth strategy relationships to biomass production with *L. balthica* additions were unexpected and contrary to previous observations of plant biomass responses to sediment nutrient enrichment (Lee & Dunton 2000, Maurer & Zedler 2002, Frazer et al. 2016). Previous evidence suggested that if *L. balthica* had supplied the plants with nutrients, then perhaps they would invest more biomass into aboveground biomass to reduce biomass limitation by light attenuation (Lee & Dunton 2000, Maurer & Zedler 2002, Frazer et al. 2016). Instead, the community growth strategy most strongly related to productivity was characterised by an investment in shoot proliferation and root architecture (Chapter III). One possible explanation is that *L. balthica* supplied the plants with carbon which affected their

internal carbon balance (Ralph et al. 2007). A previous study suggested that seagrass could potentially colonise deeper water with lower light irradiance if they had an increased carbon supply (Invers et al. 2002). Therefore, perhaps communities with *L. balthica* had a reduced necessity to capture light therefore it was more beneficial for biomass production to invest in traits such as shoot proliferation and root architecture. However, such a concept is very tentative and requires further investigation. A study which would help to clarify this greatly would be to synthesise the data from Chapters II and III then compare changes in species community composition versus changes in trait expression. Indeed, this approach would also identify whether the change in biomass production by different growth strategies was caused by the enhanced growth of species which manifested traits characterised by high shoot proliferation and low specific root lengths (SRL). However, the synthesis is necessary to clarify this aspect because if the outcome was caused by high production of certain species, then one would also expect total experimental biomass production to be higher for all communities with *L. balthica* additions. Whereas, total biomass production was not significantly different between communities with or without *L. balthica* additions.

5.6. Plant-infauna interactions and future change

This thesis provides new evidence to show that infauna affect submerged aquatic plant community trait-productivity relationships (Chapter III). Therefore, this thesis shows that infauna can affect submerged aquatic plant functioning, which supports previous evidence that they influence aquatic plant meadows (Gagnon et al. 2020). Bulleri et al. (2018) explores potential positive interactions between ecosystem engineers, such as submerged aquatic plants, and other species, such as infauna, as nature-based solutions to alleviate climate-driven environmental pressures (e.g. hypoxia). Gagnon et al. (2020) observed positive correlative relationships between temperature and positive effects by infauna to submerged seagrass. Therefore, with changing future climate (IPCC 2019), positive plant-infauna interactions could become important aspects for aquatic plant resilience to climate

change (Bulleri et al. 2018, Gagnon et al. 2020). This thesis provides important information which contributes towards management of plant-infauna interactions because its findings show ecological implications of infauna additions to mixed species aquatic plant meadows. Furthermore, the observed differences in biomass production by different community growth strategies between Chapters II and III might also have implications to plant community responses to future change. For example, the plant growth strategy related to productivity in Chapter III, which was high shoot proliferation and low SRL, might have implications to plant community responses to future changes in light availability. An opportunity to investigate this further would be to quantitatively associate plant life history strategies to the manifestation of different traits, then to measure the change in composition of plant life history strategies within a community with *L. balthica* additions. By doing this, it would be possible to infer potential long-term ecological consequences of *L. balthica* additions to plant functioning e.g. dispersal type, resilience to stressors such as temperature increase and light attenuation. Such findings would provide more mechanistic insights into the role of infauna to temperate submerged aquatic plant functioning in a changing climate.

5.7. Submerged aquatic plant traits and global plant trait syntheses

Submerged aquatic plants are under-represented and misinterpreted in global plant trait syntheses when ecological interpretations are made from global axes of trait variation. Such an argument can be supported by results of this thesis and results from previous aquatic plant trait studies (Box 1, Cambridge & Lambers 1988, Ralph et al. 2007, Gustafsson & Norkko 2019) in comparison to global plant trait syntheses (Diaz et al. 2015, 2016, Pierce et al. 2012, 2017, Kattenborn et al. 2017). Indeed, traits strongly related to aquatic plant biomass production have been misinterpreted as unimportant for submerged aquatic plants in global trait syntheses and inferences about trait function in global syntheses have been interpreted from a biased terrestrial perspective (Diaz et al. 2015,

2016, Pierce et al. 2012, 2017, Kattenborn et al. 2017). Reich et al. (2003) and Bruelheide et al. (2018) suggested that global variability of plant traits represented innate plant biomass trade-offs rather than plant responses to macro-environmental variables. This has implications to suggest that global axes of trait variability (e.g. Plant stature and resource acquisitiveness, Bruelheide et al. (2018)) are not directly related to trait function if trait function represents an interaction between a plant and its environment. This thesis, and other plant trait studies of submerged aquatic plant meadows, provide empirical evidence to support correlative inferences of global plant trait variability by Reich et al. (2003) and Bruelheide et al. (2018). The environment for submerged aquatic plants is so different to the environment of terrestrial plants that it is highly noticeable when inferences from global plant trait syntheses do not represent submerged aquatic plant ecology. Therefore, many global plant trait syntheses do not represent the ecology of all plants on Earth yet, even when submerged aquatic plant traits were included in syntheses. However, submerged aquatic plant ecology is a useful control group to test the accuracy of interpretations of correlative data using a terrestrial ecology approach. Resultantly, an opportunity for further study would be to re-evaluate global plant trait-function inferences in a collaboration between terrestrial and aquatic plant ecologists. By doing this, it might be possible for all parties to learn new insights about generalised plant functioning.

Box 1. Examples of differences in trait function between terrestrial and submerged aquatic plants

(i) Submerged aquatic plants can absorb $\delta^{13}C$ from the soil (Wetzel & Penhale 1979, Winkel & Borum 2009) and their productivity can be limited by carbon (e.g. Buapet et al. 2013). Leaf tissue $\delta^{13}C$ represents a balance between light availability, carbon availability and photosynthesis (Hu et al. 2012) as well as carbon sourcing (Smith et al. 1976). For terrestrial plants, $\delta^{13}C$ of leaf tissue represents photosynthetic rate and stomatal conductance (Scheidegger et al. 2000). Therefore, the factors affecting $\delta^{13}C$ signals are different for submerged aquatic and terrestrial plants. As a result, arguably, submerged aquatic plant $\delta^{13}C$ values should not be combined with $\delta^{13}C$ values of terrestrial plants in global plant trait syntheses, unless the research question is tentatively circumventing the ecological interpretations of $\delta^{13}C$ relationships with plant functioning.

(ii) Specific Leaf Area (SLA) is a plant functional trait which was not used for the experiments of this thesis because previous evidence suggested that it was not a potential functional effect trait to submerged aquatic plant productivity. SLA is a ratio which represents leaf area per unit leaf mass (Perez-Harguindeguy et al. 2013). It is correlated to growth rate in terrestrial plants but not for submerged aquatic plants (Cambridge & Lambers 1988). Indeed, there is limited evidence that SLA enhances light absorption by submerged aquatic plant leaves, unlike for terrestrial plants (Ralph et al. 2007). Interestingly, it can represent species-specific submerged aquatic plant responses to changes in light and carbon availability (Ralph et al. 2007, Ow et al. 2015).

5.8. Submerged aquatic plants and functional diversity

Plant functional traits have been used for many years before plant functional diversity was established as a recognised science (Garnier et al. 2016). Functional diversity indices are modern approaches which contribute towards understanding plant community ecology (Garnier et al. 2016). These indices are regularly developed and improved (e.g. Villéger et al. 2008, Mason et al. 2013, Schleuter et al. 2010), for example to incorporate intraspecific variability of functional traits (Fontana et al. 2016). Functional diversity index measurements vary depending on the calculation technique used, and there is not a right or wrong approach because indices arguably represent a concept which is unmeasurable (Schleuter et al. 2010, Garnier et al. 2016). Therefore, functional diversity indices represent the closest approximation that can be achieved, for the definition of functional diversity (see Definitions, page 10).

Functional diversity index measurements are affected by a wide variety of methodological factors (Schleuter et al. 2010 and Box 2) therefore it is imperative to interpret functional diversity indices with caution and to pay close attention to the measurement technique being used. Indeed, results from this thesis highlight the importance of taking such caution when applying functional diversity indices to plant community ecology. For example, in Chapter II functional diversity indices were improved by weighting traits according to their relationship to primary productivity using pre-existing data (Gustafsson & Norkko 2019). This improved the accuracy of functional diversity indices because it is otherwise a methodological flaw to assume that all traits have equal relationships to a process being measured (Petchey & Gaston 2006). It was an advantage of the study to be able to use pre-existing trait-productivity data from the local area for these calculations (Gustafsson & Norkko 2019), and trait weightings were justified by post-hoc linear regressions which indeed showed that some traits were more closely related to productivity than others (Chapter II). It also improved the representativeness of functional diversity indices (raised R^2 equivalent). The reason why it is important to

interpret functional diversity indices very cautiously, is that Chapter III showed that plant-trait productivity relationships were different with experimental additions of *L. balthica*. With such changes in plant trait-productivity relationships, the trait weightings used for Chapter II would have been unrepresentative of communities in Chapter III. Therefore, if functional diversity indices were calculated for Chapter III their results would have been biased to a different community growth strategy, or calculations without trait weightings would have led to different results. Consequently, functional diversity indices for Chapters II and III would have not been comparable even though the experiments were conducted in the same aquatic plant meadow with almost identical experimental designs. Indeed, functional diversity measurement results can vary widely depending on the functional diversity measurement used (Box 2, Schleuter et al. 2010, Fontana et al. 2016).

Box 2. Examples of methodological variability which lead to differences in functional diversity indices:

(i) **Multidimensional trait space calculated by convex hull or dendrogram** (Schleuter et al. 2010). Functional diversity indices are calculated by combining the variability of multiple traits, from which some common functional diversity indices are calculated. For example, functional richness represents the sum of multidimensional trait variability within a community. The multidimensional trait space can be parameterised using dendrograms or various convex hull approaches (Schleuter et al. 2010, Fontana et al. 2016). The choice of approach to calculate multidimensional trait space affects the functional diversity index being measured (Schleuter et al. 2010, Fontana et al. 2016).

(ii) **Trait selection** (Petchey & Gaston 2006). The selection of traits used to calculate functional diversity indices are pivotal for the resulting variability in functional diversity indices. The traits selected should be ecologically informed because they should represent traits that are most likely to affect a process being measured in comparison to functional diversity e.g. Primary productivity (Petchey & Gaston 2006). Trait selection varies between investigator and it can be affected by availability of data and/or resources to measure traits.

(contd.)

Box 2. (contd.)

(iii) **Trait weighting** (Petchey & Gaston 2006). Traits measured for functional diversity indices do not have equal effect sizes on a process being measured. For example, an investigator might include plant shoot density to calculate functional diversity for pollination success, but plant shoot density might not be as important for pollination as flower size. Therefore, functional diversity index accuracy can be improved by assigning relative weights to traits using pre-existing trait-process data during functional diversity calculations (Petchey & Gaston 2006). The weighting of traits and the presence/absence of trait weighting affects functional diversity index variability. This depends on the availability of pre-existing trait-process data.

This thesis has used functional diversity measurements to understand submerged aquatic plant ecology. By doing this, it has discovered novel and insightful findings about plant trait-productivity relationships and biomass production by different plant growth strategies (Chapters II & III). An important aspect about interpreting functional diversity measurements has been the importance of acknowledging the methodological context of functional diversity index calculations. Despite functional diversity index variation by calculation differences, it is still valuable to use functional diversity indices because they are powerful tools for understanding ecosystem functioning (Hooper et al. 2005, Mason et al. 2005) so long as they are applied correctly (Schleuter et al. 2010). Based on the importance of methodological context for functional diversity indices, this thesis shows that it is ecologically important to refrain from inferring generalised statements about the role of functional diversity to coastal ecosystem functioning based on findings in Chapter II. Instead, the generalised statement about functional diversity learned from this thesis is that functional

diversity experiments can be used as a pathway for gaining a variety of insights into plant community ecology. Using a functional diversity experimental approach in Chapters II and III, this thesis has been able to identify: (i) An increase in species diversity in a submerged aquatic plant meadow might increase community productivity if the introduced species manifests traits that enhance productivity (selection effect, Chapter II). (ii) Temperate submerged plant communities with high biomass production might not have a replete supply of carbon relative to plant biomass carbon requirements (Chapter II), (iii) there are three mechanisms by which aquatic plant height can enhance community productivity (Chapter II). These mechanisms are firstly increased standing biomass per unit area, increased competitive ability for height, and finally this thesis identified that competition by height increase could induce increased community productivity. Because of the suspected competition effects to productivity, plant height can have a disproportionately large effect to community productivity. Finally, the functional diversity-based experiments (Chapters II & III) showed that (iv) plant community trait-productivity relationships are labile to change within the same meadow in response to changes in environmental factors (Chapter III) because (v) infauna can affect plant trait-productivity relationships (Chapter III). These collective insights based on functional diversity experiments (Chapters II & III) contribute towards an advanced understanding of temperate aquatic plant ecosystem functioning.

6. CONCLUSION

This thesis comprises of three intensive, controlled field experiments and a high volume of laboratory and data analyses. It advocates that specific insights into plant community ecology are more valuable and generalisable than specific functional diversity indices because of methodological sources of functional diversity index variation. Findings of this thesis can be applied to a variety of other temperate submerged aquatic plant communities, including the application of insights to monocultures. Targeted research questions based on the findings of this thesis could contribute to further understand temperate submerged aquatic plant functioning including monocultures. The combined results of this thesis suggest that it could be worthwhile to commence updating context-specific submerged aquatic plant responses to sediment nutrient enrichment. With such an update from current categorical definitions to a suggested flowchart, it would be a step forwards in improving the accuracy of predictive modelling for submerged aquatic plant responses to future change. Also, results of this thesis contribute towards increasing effectiveness of future management by providing insights to infauna effects on plant functioning. This is beneficial to current restoration development because infauna additions to submerged aquatic plant meadows are an option for increasing seagrass restoration success and seagrass resilience to future change. This thesis describes how results can be applied to temperate submerged aquatic plant meadows. However, there is requirement for further research in seagrass meadows which form dense root-rhizome mattes, and this thesis describes potential options for future research. Furthermore, to understand the specific nutrient exchange mechanism between infauna and submerged aquatic plants, this thesis recommends isotope-tracing experiments and compound-specific isotope tracing experiments would provide detailed insights. This thesis has identified empirical evidence of current limitations of global plant trait syntheses and it identifies constructive steps forward to improve the global perspective of plant trait ecology. Finally, this thesis advocates the value of

insights gained from data-rich functional diversity experiments. It has used plant functional trait-process investigations to improve the collective understanding of temperate aquatic plant ecosystem functioning.

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